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Helen K. Coxall, Paul A. Wilson, Paul N. Pearson, and Philip F. Sexton

Abstract.—Digitate shell morphologies have evolved repeatedly in planktonic foraminifera throughout the Cretaceous and Cenozoic. Digitate species are usually rare in fossil and modern assemblages but show increased abundance and diversity at times during the Cretaceous and middle Eocene. In this paper we discuss the morphology and stratigraphic distribution of digitate planktonic foraminifera and establish the isotopic depth ecology of fossil ones to draw parallels with modern counterparts. $\delta^{18}O$ and $\delta^{13}C$ values of six extinct and two modern digitate species, from six time slices (Cenomanian, Turonian, Eocene, Miocene, Pleistocene and Holocene) have similar isotopic depth ecologies, consistently registering the most negative $\delta^{13}C$ and usually the most positive $\delta^{18}O$ compared to coexisting species. These results indicate a similar deep, subthermocline (>150 m) habitat, characterized by lower temperatures, reduced oxygen, and enrichment of dissolved inorganic carbon. This is consistent with water-column plankton studies that provide insight into the depth preferences of the three modern digitate species; in over 70% of observations digitates occurred in nets below 150 m, and down to 2000 m. The correlation between digitate species and subsurface habitats across multiple epochs suggests that elongated chambers were advantageous for survival in a deep mesopelagic habitat, where food is usually scarce. Increased abundance and diversity of digitates in association with some early and mid-Cretaceous oceanic anoxic events, in middle Eocene regions of coastal and equatorial upwelling, and occasionally in some modern upwelling regions, suggests an additional link with episodes of enhanced ocean productivity associated with expansion of the oxygen minimum zone (OMZ). We suggest that the primary function of digitate chambers was as a feeding specialization that increased effective shell size and food gathering efficiency, for survival in a usually food-poor environment, close to the OMZ. Episodes of increased digitate abundance and diversity indicate expansion of the deep-water ecologic opportunity under conditions that were unfavorable to other planktonic species. Our results provide evidence of iterative evolution reflecting common functional constraints on planktonic foraminifera shell morphology within similar subsurface habitats. They also highlight the potential of digitate species to act as indicators of deep watermasses, especially where there was expansion of the OMZ.

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Introduction

The fossil record of planktonic foraminifera reveals the repeated evolution of chamber shapes and shell morphologies during independent Cretaceous and Cenozoic evolutionary radiations (e.g., Berger 1969; Cifelli 1969; Frerichs 1971; Steineck and Fleischer 1978; Lipps 1979; Hart 1980; Caron and Homewood 1983; Leckie 1989; Norris 1991; Pearson 1996; Moullade et al. 2002). Identifying biotic and abiotic factors that have played a role in selection of morphologies across these radiations is a continuous goal for micropaleontologists and an important area of research for paleontology in general. However, linking planktonic ecology with shell morphology has been problematic, and isotopic data do not reveal a consistent correlation with preferred depth habitat among most common globular and compressed shell morphologies (Berger 1969; Cifelli 1969; Frerichs 1971; Lipps 1979; Hart 1980; Caron and Homewood 1983; reviews in Corfield and Cartlidge 1991, and Pearson 1998).

A conspicuous but usually rare element of planktonic foraminifera assemblages throughout the Cretaceous and Cenozoic are ''digitate'' planktonic foraminifera, i.e., forms that have one or more chambers of the adult whorl radially elongated to form distinctive fingerlike exten-

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sions. Little is known about the ecology of digitate species because of their scarcity and patchy distribution. Limited plankton-tow data (e.g., Rhumbler 1911; Bradshaw 1959; Bé 1977) have suggested an unusually deep dwelling habitat for modern digitates and a similar ecology has been predicted for fossil species on the basis of morphological similarities (e.g., Berger 1969; Cifelli 1969; Frerichs 1971; Steineck and Fleischer 1978; Hart 1980; Caron and Homewood 1983; Leckie 1989; Norris 1991; Pearson 1996; Moullade et al. 2002). Several reports have also linked digitates from the Recent, Eocene, and Cretaceous with enhanced surface ocean productivity and/or low-oxygen conditions (e.g., Bradshaw 1959; Magniez-Jannin 1998; Coccioni et al. 2006; Coxall and Pearson 2006). These observations suggest a correlation between digitate shell morphology and the environment but supporting data have been lacking. Here we test the hypothesis that digitate shell morphology is a functional specialization to a deep-dwelling ecology by comparing the isotopic paleodepth signatures of digitate species from multiple time slices. By integrating the geochemical data with stratigraphic and paleoenvironmental information, and with existing water-column plankton sampling data, we are able to explore parallels between fossil and modern counterparts and assess the paleoceanographic significance of these enigmatic forms.

Shell Function and Depth Ecology.—Determining the functional morphology of foraminifera shells is a challenge because of their small size (<1 mm), the difficulties in sustaining them under laboratory conditions, and the limitation of their fossil remains and encasing sediment to provide environmental information. Oxygen and carbon stable isotopes ($\delta^{13}C$ and $\delta^{18}O$) measured on foraminiferal shell calcite can provide valuable insights into planktonic ecology that can be used to test aspects of functional models for chamber design related to depth habitat.

The method relies on isotope fractionation processes occurring in the water column. Oxygen isotope fractionation between ambient seawater and foraminiferal calcite during calcification is temperature dependent. This means that depth-stratified foraminiferal assemblages from open-ocean sites can be expected to exhibit a trend of increasing foraminiferal $\delta^{18}O$ with depth that parallels the trend of decreasing temperature (Fairbanks et al. 1980, 1982). Species living in the warmest waters closest to the surface, therefore, register more negative $\delta^{18}O$ than deeper dwellers and bottom living (benthic) species. In contrast, foraminiferal $\delta^{13}C$ decreases with depth because of the preferential uptake of $^{12}CO_2$ during photosynthesis in the surface euphotic zone and its subsequent remineralization back into the ΣCO_2 pool by respiration at depth. As a result, dissolved inorganic carbon (DIC) in the modern surface ocean may be 1‰ to 2‰ more positive than the $\delta^{13}C$ of DIC in the deep ocean (Kroopnick 1985) and the shells of surface dwelling forms would be expected to have more positive $\delta^{13}C$ values than deeper dwellers. However, $\delta^{18}O$ and $\delta^{13}C$ values can be offset from ''equilibrium'' with ambient seawater by the effect on isotope fractionation of environmental parameters such as $[CO_3^{2-}]$ and pH (Spero et al. 1997; Zeebe 1999) or physiological processes such as symbiont photosynthesis or foraminiferal respiration (Spero and Williams 1989; Spero et al. 1991; Spero and Lea 1993, 1996; Ortiz et al. 1996). Despite these complications, which tend to affect $\delta^{13}C$ more than $\delta^{18}O$, the basic pattern of foraminiferal $\delta^{18}O$ and $\delta^{13}C$ variation with water-column depth facilitates the reconstruction of fossil foraminiferal depth habitats based on the relative stable isotope offsets between species in an assemblage (see Spero 1998; Pearson 1998; Pearson et al. 2001; Sexton et al. 2006). This method is used widely to identify foraminiferal tracers of shallow and deep watermasses on multiple geological scales.

Previous stable isotope and environmental interpretations have suggested some functional fits between various planktonic foraminifera groups but there are plenty of non-analogues. For example, the Paleogene morozovellids and Cretaceous globotruncanids had comparable ornate keeled shells and their isotopic signatures suggest they were both surface dwelling and symbiotic (Houston and Huber 1998; Norris 1996). The living species *Globorotalia menardii*, which has a keeled unornamented shell, and its Paleogene analogue *Globanomalina pseudomenardii* are or were both

deep dwellers (Hemleben et al. 1989; Olsson et al. 1999). This is where the similarities end, because the Eocene *G. menardii*-analogue *Turborotalia cunialensis* was a surface mixed layer form (Pearson et al. 2006b), whereas counterparts from the Cretaceous occurred in both shallow (*Planomalina buxtorfi*) and deeper (*Rotalipora* spp.) habitats (Wilson and Norris 2001). Among the ''globigerine'' morphotypes there are also differences in depth habitat. For example, modern *Globigerinoides sacculifer* and *G. ruber* live in shallow surface waters whereas Paleogene analogues in the genus *Subbotina* routinely register deep, probably thermocline isotopic signatures (Olsson et al. 2006a). Small triserial forms on the other hand, which occur in modern oceans and throughout the Cretaceous and Paleogene, are or were all surface dwellers, specialized to continental margin upwelling environments and unstable marine conditions generally (Kroon and Nederbragt 1990).

In many of these examples the functional comparisons are less than perfect because there are usually fine-scale differences in morphology beyond the general form (e.g., keels may be double or single, ornamentation may be built of muricae or pustules), indicating that there have been various structural convergences that may not always have similar functions in detail. The correlation between morphology and depth habitat is also far from simple, because, as in the case of the modern compressed globorotaliids, some species migrate from the surface to deeper parts of the water column during ontogeny. Digitate morphologies, however, which involve simple elongations of individual chambers, are more likely to be homologous structures and, we suppose, are more likely to have a similar function.

Materials and Methods

The stratigraphic distribution of digitate planktonic foraminifera from the Cretaceous and Cenozoic was recorded from new micropaleontological observations in deep-sea core material and the literature. Morphologies are considered digitate if one or more adult chambers are radially elongated and have an aspect ratio (chamber length divided by width at the midpoint) of 1.5 or greater. This arrangement results in widely separated chambers and deeply incised sutures giving individuals a distinctly lobate outline. We include forms with bifurcating digitate chambers, as sometimes occurs in the genus *Leupoldina* and in *Hastigerinella digitata* but exclude *Globigerinoides fistulosus*, which has multiple protuberances on individual chambers. By our definition, tubulospines, as occur in *Hantkenina* and *Schackoina*, do not alone constitute a digitate form because they are slender non-perforate projections, whereas digitate chambers are extended chambers with continuous wall texture. The exceptions to this are the earliest hantkeninids and some schackoinids that have tubulospines (or prototubulospines, e.g., *Hantkenina singanoae* [Coxall and Pearson 2006]) emerging from elongated chambers. We regard tubulospines as a different structural modification, although they may have originally served a similar function (i.e., in increasing the effective size of the foraminifera).

Evidence for the distribution and ecology of living digitate species was synthesized from the literature and unpublished observations from plankton surveys. A reconstruction of the geographic distribution of digitate species was produced for the middle Eocene, a time of high digitate diversity that is well represented in deep-sea and continental margin sediments. $\delta^{13}C$ and $\delta^{18}O$ analysis was used to investigate the paleoecologies of digitate homeomorphs from six time-slices in seven mid- to low-latitude deep-sea sites in the Atlantic and Pacific Oceans (Table 1). Preservation of foraminiferal specimens varied between sites. Cenomanian, Turonian, and Pleistocene samples show excellent (glassy) preservation (see Wilson and Norris 2001; Pearson et al. 2004; Sexton et al. 2006). Scanning electron microscope (SEM) examination reveals neomorphic recrystallization of foraminiferal calcite at the micron scale (see Sexton et al. 2006) in the Miocene and Eocene material, suggesting that the primary isotopic signal has been partially altered through diagenesis. The effect of diagenetic alteration on planktonic foraminiferal calcite close to the seafloor will be to increase oxygen isotope values, and this effect will be greatest at low latitudes (where the vertical

TABLE 1. Time slices and localities in the isotopic paleo-depth analysis.

Epoch	Biozone	Age	Locality	Lat. Long.	Lithology	Digitate taxon	Abundance
Holocene	—	—	Core CD154-07-7PK, Agulhas Current	30°07.9′S, 31°41.8′E	Orange silty foram ooze	*Beella digitata*	Rare
Late Pleistocene	—	14.2 Ka[1]	BoxC EDRC92, W. Pacific	2°13.5′S, 156°59.9′E	Foram-nanno ooze	*Globigerinella adamsi*	Rare
Middle Miocene	N10[2]	14.7–15.3 Ma	ODP Site 872, N.E. Pacific	10°6′N, 162°52′E	Foram-nanno ooze	*Clavatorella bermudezi*	Rare
Latest early Eocene	P9[3]	49–50.4 Ma	Kane-9 C-42, N.E. Atlantic	21°N, 19°W	Foram-nanno ooze	*Clavigerinella colombiana, C. akersi, C. jarvisi*	Few-common
Latest early Eocene	P9[3]	49–50.4 Ma	ODP Site 865, mid Pacific	18°26.425′N, 179°3.3′W	Foram-nanno ooze	*Clavigerinella eocanica*	Few
Late Turonian	UC9a[4,5]	88–90 Ma	DSDP Site 144, N. Atlantic	9°27′N, 54°21′W	Black shales, carbonaceous mudstones	*Clavihedbergella watersi*	Rare
Cenomanian	KS17[3]	99.1–96.8 Ma	DSDP Site 137	25°55.53′N, 27°03.64′W	Nanno marl/chalk	*''Hedbergella'' simplex*	Rare

Data sources: [1]C-14 data from Peng et al. (1979) converted to calendar years using calibration of Stuiver and Reimer (1993); [2]Pearson 1995; [3]This study, timescale and zonation of Berggren et al. (1995); [4]Wilson et al. 2002; [5]Arthur and Natland 1979.

temperature gradient in the water column is greatest and where sedimentation rates are low; Schrag et al. 1995; Rudnicki et al. 2001). Previous studies have demonstrated, however, that interspecies offsets, which we assume reflect original differences in depth habitat, are maintained despite such minor alteration, although the absolute $\delta^{18}O$ values are likely to be artificially increased and the multispecies gradient compressed (Corfield et al. 1990; Pearson et al. 2001; Sexton et al. 2006).

$\delta^{13}C$ and $\delta^{18}O$ was measured on monospecific samples of digitate morphotypes plus three or more additional taxa and a benthic species (where possible) from each assemblage representing a range of mixed-layer and deeper-water ecologies. Samples were composed of 2–25 specimens, depending on species size and abundance (Appendix). Analyses were performed at the National Oceanography Centre in the United Kingdom, using a Europa Geo 20–20 mass spectrometer equipped with a ''CAPS'' automatic carbonate preparation system and at Cardiff University on a MAT252 gas source mass spectrometer with an automated KIEL device. Results are reported relative to Vienna Pee Dee Belemnite standard (VPDB). Standard analytical precision is better than 0.1‰ for $\delta^{18}O$ and $\delta^{13}C$ for all data.

Results

Digitate Species in the Cretaceous and Cenozoic.—We recognize a minimum of 27 digitate species in 13 genera (Fig. 1), each having chamber aspect ratios of 1.5 or greater in one or more of the adult chambers (Table 2). The number of chambers in the final whorl is consistent within species but varies from 3.5 to 7 between taxa. The distal ends of the chambers also vary between species, ranging from simple and rounded (e.g., ''*Hedbergella*'' *simplex*, *Clavigerinella eocanica*, and *Clavatorella bermudezi*), to bulb-like (e.g., *Leupoldina* spp., *Clavihedbergella watersi*, *Clavigerinella akersi*) or pointed (*Clavihedbergella alexanderi*, *Clavigerinella caucasica*, and *Globigerinella adamsi*). Coiling is mostly low trochospiral or planispiral except in *Beella digitata* and *Hastigerinella digitata*, which tend to show more irregular coiling patterns. SEM imaging reveals differences

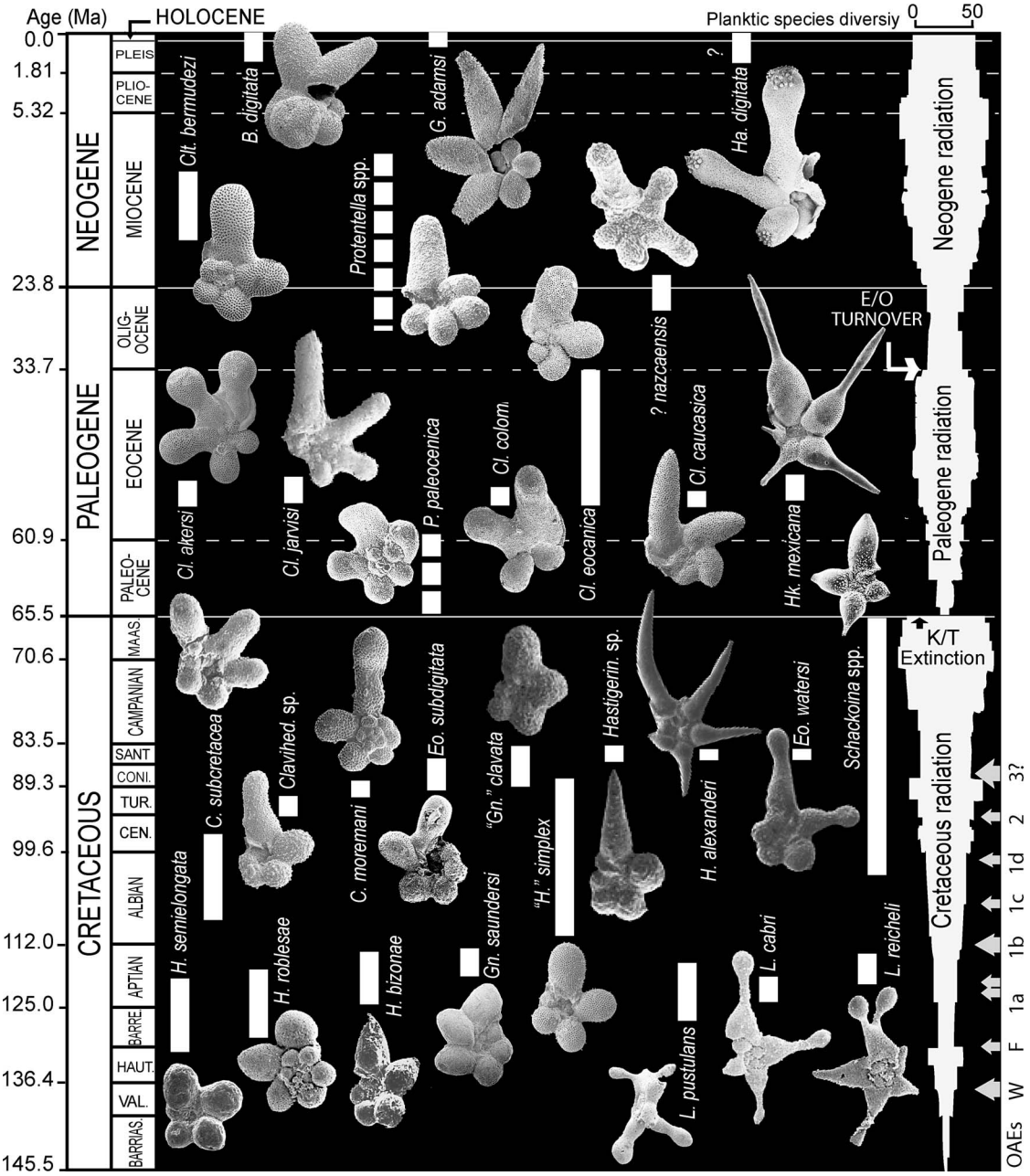

FIGURE 1. The stratigraphic distribution of living and fossil planktonic foraminifera with digitate morphologies, highlighting the iterative evolution of this morphology in successive evolutionary radiations. Foraminiferal diversity trends (right) from Norris (1991) and Leckie et al. (2002). Ranges are approximate because occurrences are sporadic. Note: The Pliocene to Holocene timescale is exaggerated. Data sources—Cretaceous: Longoria 1974; Magniez-Jannin 1998; Premoli Silva and Sliter 1999; Verga and Premoli Silva 2002; Coccioni et al. 2006; Mesozoic Planktonic Foraminifera Working Group. Paleogene: Coxall and Pearson 2006; Quilty 1976; de Klasz et al. 1987; Cicha et al. 1998. Neogene–Quaternary: Cicha et al. 1998; Kennett and Srinivasan 1983; Pearson 1995; Saito et al. 1976; Srinivasan and Kennett 1975. Generic abbreviations: *B.* = *Beella*, *C.* = *Clavihedbergella*, *Cl.* = *Clavigerinella*, *Clt.* = *Clavatorella*, *E.* = *Eohastigerinella*, *G.* = *Globigerinella*, *Gn.* = *Globigerinelloides*, *H.* = *Hedbergella*, *Ha.* = *Hastigerinella*, *Hastigerin.* = *Hastigerinoides*, *Hk.* = *Hantkenina*, *L.* = *Leupoldina*, *P.* = *Parasubbotina*. Arrows on the right identify Cretaceous oceanic anoxic events (OAEs) of the Mediterranean Tethys (after Coccioni et al. 2006). W = Weissert, F = Faraoni. Ages of stage boundaries (left) are from Gradstein and Ogg (2004) for the Cretaceous and from Berggren et al. (1995) for the Cenozoic.

TABLE 2. Aspect ratios of forms with elongated chambers measured in mm from Figure 1. Species marked with * are not considered ''digitate'' because their adult chamber aspect ratios are less than 1.5.

Species	Final chamber height	Final chamber width	Final chamber aspect ratio	Penultimate chamber height	Penultimate chamber width	Penultimate chamber aspect ratio
Hastigerinella digitata	27.0	6.0	4.5	25.0	6.0	4.2
Globigerinella adamsi	28.0	6.0	4.7	26.0	7.0	3.7
Beella digitata	20.0	7.5	2.7	18.0	11.0	1.6
Protentella spp.	21.0	9.0	2.3	11.0	5.0	2.2
Clavatorella bermudezi	19.0	10.0	1.9	13.0	5.0	2.6
''Clavigerinella'' nazcaensis	18.0	7.0	2.6	14.0	6.0	2.3
Clavigerinella eocanica	17.0	9.0	1.9	11.0	6.0	1.8
Parasubbotina paleocenica	17.5	12.0	1.5	13.0	8.0	1.6
Clavigerinella akersi	16.0	6.0	2.7	16.0	6.0	2.7
Clavigerinella jarvisi	26.0	7.0	3.7	17.0	6.0	2.8
Clavigerinella colombiana	18.0	7.0	2.6	17.0	7.0	2.4
Clavigerinella caucasica	26.0	7.0	3.7	16.0	7.0	2.3
Hantkenina mexicana	17.0	10.0	1.7	12.0	7.0	1.7
Clavihedbergella subcretacea	15.0	7.0	2.1	15.0	7.0	2.1
Eohastigerinella watersi	23.0	6.0	3.8	15.0	5.0	3.0
Hedbergella alexanderi	30.0	5.0	6.0	21.0	4.0	5.3
Eohastigerinella subdigitata	15.0	6.0	2.5	11.0	7.0	1.6
''Globigerinelloides'' clavata	14.0	9.0	1.6	10.0	9.0	1.1
Hastigerinoides sp.	24.0	7.0	3.4	10.0	9.0	1.1
Schackoina multispinata	15.0	6.0	2.5	10.0	5.0	2.0
Clavihedbergella moremani	21.0	7.0	3.0	11.0	6.0	1.8
Clavihedbergella sp.	19.0	6.0	3.2	11.0	7.0	1.6
Leupoldina reicheli	15.0	5.0	3.0	14.0	7.0	2.0
Leupoldina cabri	22.0	3.0	7.3	18.0	3.0	6.0
Leupoldina pustulans	12.0	3.5	3.4	12.0	3.0	4.0
Hedbergella bizonae	17.0	8.0	2.1	10.0	8.0	1.3
''Hedbergella'' simplex	15.0	7.0	2.1	11.0	7.0	1.6
*Globigerinelloides saundersi**	12.0	9.0	1.3	11.0	8.0	1.4
*Hedbergella roblesae**	12.0	13.0	0.9	14.5	11.5	1.3
*Hastigerinella semielongata**	17.0	12.0	1.4	15.0	11.5	1.3

in wall texture between homeomorphs, varying from smooth or weakly cancellate and probably sparsely spinose (*Clavigerinella* [Coxall and Pearson 2006]) to honeycomb-spinose (*Globigerinella*, *Beella*), monolamellar, triradiate-spinose (*Hastigerinella*) (Saito et al. 1976; Hemleben et al. 1989), microperforate (*Leupoldina* [Verga and Premoli Silva 2002]), and smooth pustulose (*Hedbergella*, *Globigerinelloides*, and *Clavihedbergella* [BouDagher-Fadel et al. 1997; Wilson et al. 2002; Mesozoic Planktonic Foraminifera Working Group 2006]). These wall textures define independent phylogenetic groups that evolved during successive evolutionary radiations (e.g., Olsson et al. 1999; BouDagher-Fadel et al. 1997; Moullade et al. 2002) and highlight the convergence on the digitate form. In *B. digitata*, only one or two chambers are elongated and the degree of elongation varies significantly between specimens.

Digitate morphologies first appeared midway through the Early Cretaceous (Barremian–Aptian) and occur throughout the remainder of the Cretaceous and Cenozoic with three species living today (Fig. 1). None survived the K/T extinction or late Eocene turnover that define the bases of the major epoch-spanning evolutionary radiations. They were most diverse in the Aptian (eight species), the Turonian to Santonian (eight species) and the latest early middle Eocene (six species). They were less diverse in the Paleocene, late Eocene to early Oligocene, and most of the Neogene. This may reflect lack of study or climatically driven changes in pelagic environments over time that influence the occurrence of digitate species. The list of taxa presented in Figure 1 may not be exhaustive by some workers' standards because of the different taxonomic schemes currently in use. Cretaceous taxonomy, especially, is less stable than that of the

Cenozoic (see BouDagher-Fadel et al. 1997; Moullade 2002) but most workers accept the generic classification of Loeblich and Tappan (1988), separating planispiral clavate (*Eohastigerinella*), planispiral tapering (*Hastigerinoides*), and trochospiral clavate (*Clavihedbergella*) (B. Huber personal communication 2007), and Figure 1 has been constructed to reflect this scheme. Despite differences in taxonomic opinion, we believe that the list is largely representative of the generic and specific diversity across epochs and should therefore capture the essence of the stratigraphic distribution of taxa exhibiting digitate morphologies. Moreover, our definition of digitate form (i.e., elongate chamber(s) with an aspect ratio greater than 1.5) will exclude some taxa that other workers may consider digitate (e.g., *Hedbergella bollii*, *Clavihedbergella sigali*) (Table 2). There are also other genera, e.g., *Protentella*, that may meet our criteria for being digitate but whose specific diversity is still unresolved.

Ecology of Living Digitate Species.—There are three digitate species living today, *Globigerinella adamsi* (Banner and Blow 1959), *Beella digitata* (Brady 1879), and *Hastigerinella digitata* (Rhumbler 1911). None have been observed alive in the laboratory and only limited information is available on their ecology and environmental preferences. All three species are restricted to the low and mid latitudes (Table 3) and are typically rare in open-ocean watermasses and underlying sediments. *Beella digitata* is more common than *G. adamsi* and *H. digitata* and occurs throughout the Atlantic and Mediterranean (Gross 2001; Hemleben et al. 1989), whereas the latter two species are thought to be mostly restricted to the Indian and Pacific Oceans (Bradshaw 1959; Bé and Tolderlund 1971). Because of its delicate monolamellar shell wall, *H. digitata* has an extremely low preservation potential and is rarely seen in sediments (Hilbrecht 1996). There are several records, however, of modern digitate species occurring at unusually high abundance levels (5–10% of assemblage), e.g., abundant *G. adamsi* in the South Pacific region (Brady 1884), west-central Equatorial Pacific, and off Japan (Bradshaw 1959). In addition, numerous *H. digitata* have been recorded on video film by a remotely operated submersible vehicle (ROV) in Monterey Bay, California (S. Haddock, MBARI, unpublished), a region that is known for the strong seasonal upwelling and pronounced oxygen minimum conditions. None of these unusual occurrences, however, have been systematically studied and presently they provide little information about the environmental preferences of modern digitate species.

Rare observations of digitate species in plankton studies reveal deep habitats, usually below 200 m; in over 70% of observations digitates occurred in nets below 150 m, and sometimes as deep as 2000 m (Table 3). The Monterey Bay ROV observations also support a deep habitat for *H. digitata*, with concentrations observed at depths of approximately 200 m, i.e., below the base of the seasonal thermocline (S. Haddock personal communication 2002). Examination of ingested material in rare captured specimens suggests that *H. digitata*, like its close relative *H. pelagica*, is strictly carnivorous (Rhumbler 1911; C. Hemleben personal communication 2005), whereas *B. digitata* and *G. adamsi* are thought to be omnivorous (C. Hemleben personal communication 2005). Symbionts have not been observed in *H. digitata* or *B. digitata* (M. Kucera personal communication 2007). No information is available on symbiotic associations of *G. adamsi*.

Although usually restricted to the low and mid latitudes, *B. digitata* has been reported in Pleistocene sediments from the Rockall Channel, ~60°N (northeast Atlantic) (Holmes 1984), together with a second species of *Beella*, *B. megastoma* Earland. However, the specimens of *B. digitata* illustrated by Holmes (1984: p. 102, Pl. 1, Figs. 6, 7) do not possess the radially elongate chambers characteristic of *B. digitata* sensu stricto (i.e., with adult-chamber aspect ratios of 1.5 or greater), suggesting that these high-latitude forms represent morpho- and ecotypes different from the extreme digitate forms found at lower latitudes. Interestingly, abundance spikes of *B. megastoma* in the Norwegian-Greenland Sea have been correlated with meltwater pulses associated with late Pleistocene glacial terminations (Bauch 1994). Although these northerly occurrences of *Beella* spp. are clearly of paleoceanographic interest,

TABLE 3. Depth occurrence of modern digitate planktonic foraminifera from plankton tows. Records are from the literature and unpublished information.

Site	Lat.	Long.	Plankton tow bottom depth (m)	Plankton tow top depth (m)	Species	Source
Equatorial Pacific	?	?	50	23	*Beella digitata*	Watkins 2003
Arabian Sea, NIOP-310-5-3	52.73°N	16.02°E	49	23	*Beella digitata*	Peeters & Brummer 2002
Arabian Sea, NIOP-310-5-1	52.73°N	16.02°E	100	74	*Beella digitata*	Peeters & Brummer 2002
Arabian Sea, NIOP-310-6-4	52.73°N	16.02°E	148	98	*Beella digitata*	Peeters & Brummer 2002
Arabian Sea, NIOP-310-6-3	52.73°N	16.02°E	200	148	*Beella digitata*	Peeters & Brummer 2002
Arabian Sea, NIOP-310-6-1	52.73°N	16.02°E	98	49	*Beella digitata*	Peeters & Brummer 2002
Arabian Sea, NIOP-917-1-3	52.92°N	15.89°E	203	153	*Beella digitata*	Peeters & Brummer 2002
Arabian Sea, NIOP-917-1-2	52.92°N	15.89°E	302	203	*Beella digitata*	Peeters & Brummer 2002
Arabian Sea, NIOP-920-1-2	52.64°N	16.08°E	303	202	*Beella digitata*	Peeters & Brummer 2002
Arabian Sea, NIOP-920-1-1	52.64°N	16.08°E	501	303	*Beella digitata*	Peeters & Brummer 2002
Mediterranean	?	?	200	100	*Beella digitata*	M. Kucera pers. comm. 2006
Mediterranean	?	?	300	200	*Beella digitata*	M. Kucera pers. comm. 2006
Mediterranean	?	?	500	300	*Beella digitata*	M. Kucera pers. comm. 2006
Mediterranean	?	?	700	500	*Beella digitata*	M. Kucera pers. comm. 2006
N.W. Arabian Sea Site 308-1-3	52.5°N	16.14°E	72	48	*Globigerinella adamsi*	Peeters & Brummer 2002
N.W. Arabian Sea Site 922-2-2	52.52°N	16.17°E	77	52	*Globigerinella adamsi*	Peeters & Brummer 2002
E. Indian Ocean	05°58′S	90°00′E	200	—	*Globigerinella adamsi*	Bé 1977
US Fish & Wildlife Service, Pacific Oceanic Fisheries Invest. Station D	33°02′N	118°23′W	400	—	*Globigerinella adamsi*	Bradshaw 1959
Challenger Station, Ki Islands, E. Archipelago, Pacific (not *G. digitata* as stated)	~20°N	~168°E	1061 (580 fathoms)	—	*Globigerinella adamsi*	Brady 1884
Pacific -Biotrawl V18 SBT 116	12°13′S	160°58′E	2138	2177	*Globigerinella adamsi*	Saito et al. 1976
Atlantic	13°31′N	18°03′W	10	10	*Hastigerinella digitata*	Bé 1977
Monterey Bay	36.5°N	122.2°W	~200	—	*Hastigerinella digitata*	S. Haddock pers. comm.
Mediterranean	?	?	200	100	*Hastigerinella digitata*	M. Kucera pers. comm. 2006
Mediterranean	?	?	300	200	*Hastigerinella digitata*	M. Kucera pers. comm. 2006
Indian Ocean	04°07′N	80°44′E	360	—	*Hastigerinella digitata*	Bé 1977
US Fish & Wildlife Service, Pacific Oceanic Fisheries Invest. Station D	33°02′N	118°23′W	400	—	*Hastigerinella digitata*	Bradshaw 1959

TABLE 3. Continued.

Site	Lat.	Long.	Plankton tow bottom depth (m)	Plankton tow top depth (m)	Species	Source
Mediterranean	?	?	500	300	*Hastigerinella digitata*	M. Kucera pers. comm. 2006
Mediterranean	?	?	700	500	*Hastigerinella digitata*	M. Kucera pers. comm. 2006
"Humboldt Plankton Expedition"	?	?	800	600	*Hastigerinella digitata*	Rhumbler 1911
Atlantic	05°08′N	42°24′W	800	—	*Hastigerinella digitata*	Bé 1977
"Humboldt Plankton Expedition"	?	?	2000	—	*Hastigerinella digitata*	Rhumbler 1911
Beebe Station 1200, N. Atlantic	?	?	1097 (600 fathoms)	1097	*Hastigerinella digitata*	Banner & Blow 1960
Pacific: "Off San Diego" deep plankton haul	32°N	117°W	"Deep"	—	*Hastigerinella digitata*	Bradshaw 1959
Deep tow, junction of Kuroshio and Oyashio Currents	~30°N	~135°E	"Deep"	—	*Hastigerinella digitata*	Bradshaw1959

we suggest they are unrelated to the distributional patterns of *B. digitata* s.s. and do not consider them further in this paper.

This collection of observations provides only limited insights into the ecology and distribution of modern digitate species. However, the available evidence suggests a consistently deep dwelling habitat (>200 m) below the thermocline, for all living digitate species during some stage of the life cycle.

Stable Isotope Paleoecologies.—Figure 2 shows $\delta^{18}O$ and $\delta^{13}C$ values of fossil digitate species compared to other planktonic and benthic species (unadjusted) in the same sample from six time slices at seven different deep-sea sites. Interspecies offsets are assumed to reflect original differences in depth habitat, with the deep dwellers registering higher $\delta^{18}O$ and lower $\delta^{13}C$ than surface dwellers. The differences in absolute and relative $\delta^{18}O$ reflect regional differences in surface-water (planktonics) and deep-sea (benthics) temperature, degree of thermal stratification, and depth of the thermocline (Berger et al. 1978; Arthur and Natland 1979; Bralower et al. 1995). Minor diagenetic alteration may also contribute to increased absolute $\delta^{18}O$ values and an artificially compressed multispecies gradient in material from ODP Sites 865 and 872 and Kane-9 Piston Core. $\delta^{13}C$ differences reflect patterns of global carbon storage, local productivity, and deep-water circulation.

Despite site-to-site isotopic differences, the relative depth ranking of digitate species analyzed is very similar in each time slice. Cretaceous, Eocene, Miocene, Pleistocene, and Holocene digitate forms consistently register the highest or close to the highest $\delta^{18}O$ values (implying the coolest calcification temperatures) and usually the lowest $\delta^{13}C$ of all planktonic foraminifera. This finding is consistent with limited isotopic data from previous investigations into Eocene and Miocene digitate species (Pearson et al. 1993; Coxall et al. 2000, 2003 on *Clavigerinella*; Pearson and Shackleton 1995 on *Clavatorella bermudezi*) that suggest a deep-dwelling habitat.

Distribution of Eocene Digitate Forms.—The middle Eocene was a time of increased digitate diversity, with up to six species of *Clavigerinella* and several species of *Hantkenina* with

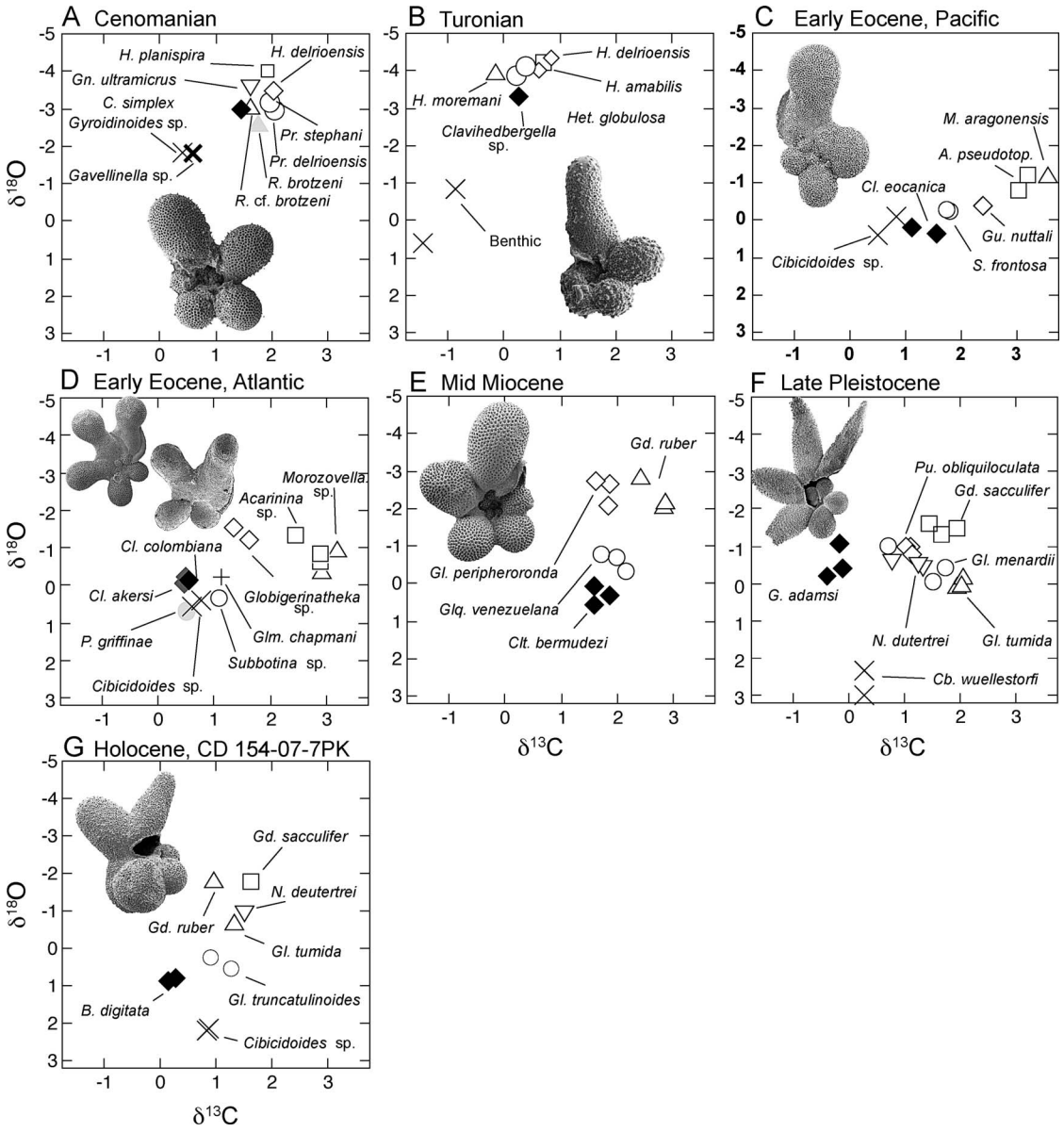

FIGURE 2. Multispecies stable isotope arrays from six time slices (seven sites) showing the relative isotopic depth-ranking of digitate homeomorphs (black and gray diamonds) compared with co-occurring planktonic and benthic species (where possible). A, DSDP Site 137-12-5, 4–6 cm. B, DSDP 144A-6R-1, 141–142.5 cm, data from Wilson et al. (2002). C, ODP 865C-8H-3, 70–110 cm. D, Kane-9 Core-42, 470 cm. E. ODP 872C-9H-3, 95–97 cm. F, Box ERDC-92-5, 22–23 cm, data from Berger et al. (1978) except *G. adamsi*, which are new. Note: Variation in $\delta^{18}O$ and $\delta^{13}C$ between sites reflect inter-basin and temporal differences in seawater isotopic composition. Generic abbreviations: *A. = Acarinina*,* *B. = Beella*, *C. = Clavihedbergella*, *Cb. = Cibicidoides*, *Cl. = Clavigerinella*, *Clt. = Clavatorella*, *G. = Globigerinella*, *Gd. = Globigerinoides*,* *Gl. = Globorotalia*, *Glm. = Globanomalina*, *Glq. = Globoquadrina*, *Gn. = Globigerinelloides*, *Gu. = Guembelitrioides*, *H. = Hedbergella*,* *Het. = Heterohelix*,* *M. = Morozovella*,* *N. = Neogloboquadrina*, *P. = Parasubbutina*, *Pr. = Praeglobotruncana*, *Pu. Pulleniatina*, *R = Rotalipora*, *S = Subbotina*. *Inferred or known surface dwellers (Wilson et al. 2002; Boersma et al. 1987; Pearson 1998; Berger et al. 1978; Hemleben et al. 1989). Data are presented in Appendix 1.

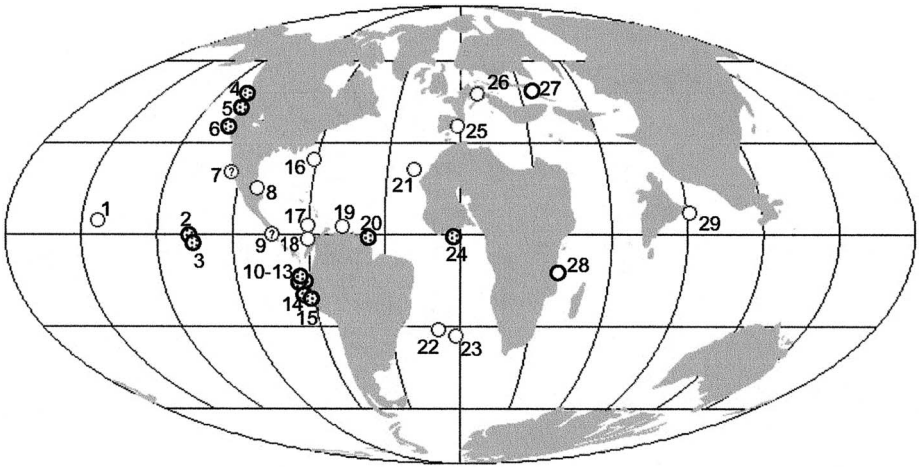

FIGURE 3. Distribution of *Clavigerinella* spp. during the middle Eocene (46 Ma base map). The map was constructed using the method outlined by Ziegler et al. (1985). Stippled fill indicates records where *Clavigerinella* spp. were found at unusually high abundance levels (>10% of assemblage). The sediments in other *Clavigerinella* localities are foraminiferal oozes with higher species diversity more typical of the low latitudes. Questions marks identify records where other microfossil and host sediment characteristics are unknown. *Clavigerinella*-rich samples typically contain only a few other species of planktonic foraminifera (e.g., *Parasubbotina* spp.) but are usually rich in radiolaria. See Table 4 for key to localities and data sources.

elongate chambers recognized. This time interval is relatively well represented in deep-sea and land sections and we have been able to produce a paleogeographic reconstruction of *Clavigerinella* spp. in order to explore the possible environmental controls on its distribution. The reconstruction was produced using 29 records compiled from new observations and the literature (Fig. 3). Paleo-coordinates of the Eocene localities are presented in Table 4. The reconstruction shows that *Clavigerinella* spp., comprising *C. eocanica*, *C. akersi*, *C. jarvisi*, *C. caucasica*, and *C. colombiana*, is restricted to the mid and low latitudes. Records are concentrated along segments of continental margin (mostly western boundaries) and the equatorial Pacific, with fewer occurrences in fully open ocean regions. In 12 localities *Clavigerinella* sp. was recorded as being unusually abundant (>10% planktonic assemblage) and occurred in association with radiolarian-rich sediments, suggesting high surface-water nutrient availability. Today these regions are characterized by high productivity due to upwelling; an atmospheric general circulation model suggests similar high-productivity conditions prevailed during Eocene time (Huber and Sloan 2000).

Discussion

Depth Ecology.—Our $\delta^{18}O$ and $\delta^{13}C$ data suggest that all the fossil digitate species investigated calcified their shells in a relatively cool watermass with high DIC content, as occurs below the surface mixed layer. The occurrence of modern digitates in deep-towed plankton nets supports this interpretation. The deep chlorophyll maximum, situated within or just below the thermocline, represents a possible habitat for digitate species that provides food at depth. Deep chlorophyll maxima, however, are widespread features in much of the world's oceans and should support larger populations of digitates than are observed. Therefore, we suggest that digitate species have more-specialized deep water ecologies defined by physio-biological structures unfavorable to most planktonic foraminifera species. The typical scarcity of digitates in deep-sea records is consistent with this hypothesis because fewer pelagic organisms live below the mixed layer outside of chlorophyll maxima, and even fewer in the mesopelagic zone (200–2000 m), where food is usually scarce compared to the epipelagic zone (0–200 m) (Gage and Tyler 1991; Wishner et al. 1995; Gowing and Wishner 1998).

TABLE 4. Reconstructed middle Eocene coordinates of the *Clavigerinella*-localities mapped in Figure 3.

ID	Locality	Palaeolat.	Palaeo-long.	Source
1	ODP Site 865, Alison Guyot	4	−143	This study
2	ODP Site 1218, Equatorial Pacific	0	−107	Lyle et al. 2002
3	DSDP Site 42, Equatorial Pacific	−3	−106	McManus et al. 1970
4	Oregon Southern Coast Range, Elkton/upper Tyee Fm.	49	−98	McKeel & Lipps 1975
5	Oregon Coast Range Tyee, Yamhill & Nestucca Fms.	42	−104	McKeel & Lipps 1972
6	Mount Diablo, California	35	−104	Church 1931; Clark & Campbell 1942
7	Santa Cruz Mts., California, San Lorenzo Fm.	20	−94	Poore & Brabb 1977
8	Veracruz, Mexico, Aragon Fm.	20	−76	Nuttall 1930
9	Arroyo San Carlos, Carmen de Bolivar Pste., Colombia, Chengue Fm.	0	−74	This study
10	Guayaquil, Ecuador	−13	−64	Stainforth et al. 1948
11	San Cristobal, Peru, Talara & Sechura Fms.	−13	−66	Cruzado Castaneda 1985
12	Parinas, Peru, Talara & Sechura Fms.	−13	−68	Cruzado Castaneda 1985
13	El Alto, Lobitos, Peru	−15	−65	Cruzado Castaneda 1985
14	ODP Site 683, Peru Continental margin	−18	−64	Suess et al. 1988
15	Basal Salina, Peru, Chacra & Talara Fms.	−21	−61	Cruzado Castaneda 1985
16	DSDP Site 390, Blake Nose	24	−61	Benson et al. 1978
17	DSDP Site 150, Aruba Gap, Venezuela	3	−60	Premoli Silva & Bolli 1973
18	Dept. of Bolivar, Colombia	−1	−60	Petters 1954
19	San Fernando, Trinidad	4	−49	Bolli 1957
20	ODP Site 1258, Demerara Rise	−1	−40	Erbacher et al. 2004
21	Kane-9 Piston Core, Endeavor Seamount	21	−19	This study
22	DSDP Site 21, Rio Grande Rise	−31	−9	Saito et al. 1976
23	DSDP Site 523, S. Atlantic	−33	−2	Hsü et al. 1984
24	ODP Site 960, Côte d'Ivoire	−1	−3	Mascle et al. 1996
25	Alicante, S. Spain	31	3	Cremedes Campos 1978
26	Mattsee, Austria, Helveticum Section	47	8	Gorbandt 1967; this study
27	Northern Caucasus Mts., Russia	48	36	Subbotina 1958
28	Kilwa, Masoko, Tanzania	−12	40	Pearson et al. 2004
29	Khasi Hills, Assam, S. India	7	91	Samanta 1973

Upwelling and Oxygen Minimum Conditions.—Increased abundance and diversity of digitate species in the Cretaceous and middle Eocene, and in restricted regions today, indicate that the digitate ecologic opportunity can be expanded at times. Examination of these concentrations of digitates should provide further insight into their ecology.

Cretaceous digitate species occurred in warm epicontinental sea localities as well as in the deep sea (e.g., Eicher and Worstell 1970; Longoria 1974; Masters 1977; Premoli Silva et al. 1999) (Fig. 1). Unusually diverse assemblages have been found in association with organic-rich sediments preserved on continental margins that are the hallmark of Cretaceous oceanic anoxic events (OAEs) (e.g., Magniez-Jannin 1998; Aguado et al. 1999; Cobianchi et al. 1999; Premoli Silva et al. 1999; Luciani et al. 2001; Leckie et al. 2002; Verga and Premoli Silva 2002; Coccioni and Luciani 2004, 2005; Coccioni et al. 2006). OAEs involved severe perturbations to the marine carbon system and pelagic ecosystems and in some cases were accompanied by extinction of many surface-living planktonic foraminifera (Leckie et al. 2002; Coccioni et al. 2006). Their cause is widely debated. One theory is that tectonic events and widespread transgressions led to stagnation of deep waters and creation of a large number of salinity-stratified marginal basins (Erbacher et al. 2001). Another is that bottom-water and water-column dysoxia resulted from intensified surface productivity related to active submarine volcanism (e.g., Schlanger and Jenkyns 1976; Premoli Silva et al. 1999; Leckie et al. 2002; Jenkyns 2003). The most widespread OAEs—the Faraoni, OA1a, and OA2—are thought to have involved extensive eutrophication (Leckie et al. 2002; Coccioni et al. 2006). These are also the times when digitate species were most abundant and diverse (Coccioni et al. 2006). The association has led to the suggestion that digitate species were specialists of

low-oxygen environments (e.g., BouDagher-Fadel et al. 1997; Magniez-Jannin 1998; Aguado et al. 1999; Cobianchi et al. 1999; Premoli Silva et al. 1999; Luciani et al. 2001; Coccioni and Luciani 2004, 2005; Coccioni et al. 2006).

Digitates were also unusually diverse in the middle Eocene (six species). There were no sedimentary equivalents to the Cretaceous OAEs during this time but *Clavigerinella* spp. occurrence shows a correlation with increased marine productivity in regions of coastal and equatorial upwelling (Fig. 3). There is no direct evidence for intensified oxygen-minimum conditions preserved in these regions (i.e., in the form of increased sedimentary organic carbon), but pronounced OMZs may have been features of these environments, as they are in modern upwelling regions (e.g., Wishner et al. 1995), even if there is no record in sediments. It seems logical that usually rare deep-dwelling digitate species would proliferate during times of high productivity because of increased food sinking out of the surface layer. However, surface productivity cannot be the principal control on digitate distribution because, besides the Cretaceous, middle Eocene, and Monterey Bay occurrences, digitate species have not been reported widely in typical modern or early Neogene upwelling systems (e.g., Arabian Sea and Benguela Current) (Prell and Curry 1981; Summerhayes et al. 1992; Little et al. 1997; Reichart et al. 1998). Therefore, specialization to OMZ conditions, which may be a consequence of increased surface productivity, and which would be unfavorable to most planktonic species, seems plausible. A closer look at the anatomy of OMZs reveals the hostilities faced by pelagic organisms and provides clues to their potential attraction.

OMZs are ubiquitous and persistent features of midwater depths in much of the world's ocean but they may become expanded through heightened marine productivity or reduced water-column ventilation (Wishner et al. 1995). Although plankton biomass and diversity are dramatically reduced within OMZs because of the limitations on aerobic respiration, plankton may become abundant at the ''redoxcline,'' the level at the base of the OMZ (400 to 1100 m) where oxygen levels begin to increase. High concentrations of organic particles and bacteria at the redoxcline provide an abundant food source to deep-dwelling plankton (Wishner and Gowing 1992; Wishner et al. 1995; Gowing and Wishner 1998). Although no records of planktonic foraminifera have been obtained so far, it is possible that deep-dwelling species, such as the digitates, can survive in these environments, feeding directly on bacteria and organic particles or preying on the primary consumers of microbes, e.g., copepods. This hypothesis is consistent with distribution patterns of digitates associated with Cretaceous OAEs; digitate species were absent from the core of the OAEs where minimum oxygen levels would have prevented aerobic respiration, but they diversified during the recovery phase (Coccioni et al. 2006), perhaps as oxygen levels began to increase but food availability remained high. Digitates may have been able to respond quickly to this expanding deep-water ecological opportunity because of their existing tolerance of hostile deep-water conditions.

The unusually low shell $\delta^{13}C$ values seen in some digitate species, e.g., *Clavigerinella* spp. *G. adamsi*, and *B. digitata*, which are always lower than in other planktonic species and sometimes lower than in co-occurring benthics, are consistent with this hypothesis because water-column $\delta^{13}C$ values reach a minimum within the OMZ (Fig. 4). However, given that foraminiferal shell carbon isotope values usually reflect a mixed signal of seawater $\delta^{13}C$ and physiological fractionation effects (e.g., Zeebe 1999; Ortiz et al. 1996; Norris 1998; Spero 1998), it is possible that the depleted $\delta^{13}C$ values are the result of a vital effect. One way of enriching ^{12}C is incorporation of metabolic CO_2 into test calcite, although this effect has previously been recorded only in surface forms such as *Globigerina bulloides* and *Globigerinella siphonifera*, which tend to have unusually high feeding rates (e.g., Spero and Lea 1996; Bijma et al. 1998). Shell calcite isotopic depletion might also be achieved by feeding on an isotopically ''light'' food source, e.g., bacteria; it is possible that, as has been demonstrated for other mesopelagic microplankton (Wishner et al. 1995; Gowing and Wishner 1998), a large part of the forams' diet at these

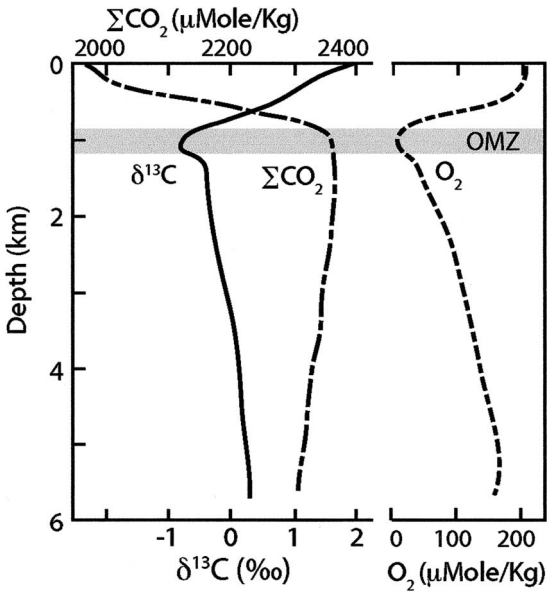

FIGURE 4. **A**, Typical vertical profile of seawater dissolved inorganic carbon (ΣCO_2), $\delta^{13}C$, and dissolved O_2 from the North Pacific (Kroopnick 1985) to aid interpretation of carbon isotopes. OMZ, oxygen minimum zone.

depths was derived from bacteria-dependent food chains, whose biosynthetic pathways result in ^{13}C-depleted organic matter (e.g., Hayes 2001). Because it is difficult to imagine that ^{13}C depletion through physiological fractionation effects would occur to a similar extent in multiple independently evolved digitate homeomorphs, we suggest that the $\delta^{13}C$ is primarily an environmental signal.

These various strands of evidence support a connection between digitate species and oxygen minimum zones but this cannot be the full story because not all OMZ environments are associated with digitate species. A possible explanation for why *H. digitata* is common in Monterey Bay but not other upwelling regions is that the low-oxygen watermass off California and the eastern Pacific is more or less permanent, whereas the low-oxygen conditions in the Arabian Sea and Benguela systems are highly seasonal. If digitate species were slow in maturing, low population densities might have prevented their persistence where the OMZ is seasonal. The lack of evidence for digitate evolution during episodes of increased organic-matter accumulation associated with Plio-Pleistocene sapropels (e.g., Rohling 1994; Rohling et al. 2004) may reflect differences in the causal mechanisms of the oceanic dysoxia and its effect on deep-dwelling plankton associated with the late Neogene events as compared to the Cretaceous OAEs.

Data are lacking for the Oligocene and Miocene but available records suggest that digitate species were less common from the late Eocene onward and they have never been as abundant or diverse as they were during the early Aptian, Albian, and late Cenomanian (Coccioni et al. 2006). This may be because periods of sustained and expanded OMZ conditions, which occurred more frequently under greenhouse climates because of reduced water-column stratification and increased volcanic input of biologically limiting nutrients (Leckie et al. 2002), became less frequent as crustal production slowed and thermal and density stratification of the surface ocean increased under the evolving icehouse climate system.

Functional Significance of Digitate Chambers.—Our results suggest that digitate morphologies were maintained in planktonic foraminifera populations exposed to similar environmental constraints. One possibility is that elongation of individual chambers is efficient for survival in persistently low-oxygen environments by increasing shell surface area for improved gas transport, as has been proposed for Cretaceous species of the OAEs (e.g., BouDagher-Fadel et al. 1997; Magniez-Jannin 1998; Aguado et al. 1999; Cobianchi et al. 1999; Luciani et al. 2001; Coccioni and Luciani 2004, 2005; Coccioni et al. 2006). The problem with this hypothesis is that there is almost no experimental evidence to support the idea that gas exchange occurs across the shell surface, aside from the observation that pores are associated with concentrations of mitochondria, which in turn are associated with gas transport. In addition, if gas transport is the issue, flattened discoidal shells might be expected to provide a geometrically more efficient body plan. Moreover, not all digitate species show associations with low-oxygen environments. Even among the Cretaceous species associated with OAEs, digitates are absent from the core of the events and diversify in parallel with some non-digitate species, suggesting that ad-

ditional factors control their distribution besides oxygen availability (Coccioni et al. 2006).

A more likely explanation is that radial chamber elongation was efficient for feeding in a subsurface habitat where the food supply was sparse and/or irregular. Elongate chambers may function as ''fishing rods,'' supporting long food-gathering rhizopods (strands of cytoplasm) that increase the effective shell size and volume of water that could be searched for food at minimum metabolic cost (R. D. Norris personal communication 2001). Radial elongation allows digitate species to attain unusually large shell sizes; the sizes of *Clavigerinella* spp. and *Clavatorella bermudezi*, commonly ~500 mm, and of *H. digitata*, up to 2 mm, are consistent with this hypothesis. Effective shell size is further increased in some digitate species by the presence of fine calcitic spines; e.g., *H. digitata* has spines emerging from the tips of individual chambers, creating a radiating net that more than triples the radius. The purpose of these spines is very likely to provide additional support for rhizopods and to help secure large prey items. *Beella digitata* and *G. adamsi* are also spinose and may have had similar arrangements of spines, although live specimens have not been observed. Spines were absent in Cretaceous and possibly most Paleogene digitate forms. Gas exchange efficiency under low-oxygen conditions may also have been improved as a consequence of having digitate chambers.

Although digitate species appear to be exclusively deep dwelling, digitate form is not a prerequisite for subsurface living because there are a number of other species with observed or inferred deep dwelling habitats that do not have elongated chambers e.g., Paleogene and Neogene *Globorotaloides* spp., including living *G. hexagona* (Ortiz et al. 1996), and Paleogene *Parasubbotina* spp. (Olsson et al. 2006b). However, the evolution of some digitate species may have occurred within a subsurface habitat in response to changing physical chemical and nutrient structures. This hypothesis is consistent with phylogenetic reconstructions that suggest that acquisition of digitate chambers in some groups involved parapatric speciation, with digitate species evolving from existing deep dwellers (e.g., *C. bermudezi* from *Globorotaloides hexagona* (Fleisher 1974) and *C. eocanica* from *Parasubbotina eoclava* (Coxall et al. 2003)). Moreover, loss of elongated chambers in the tubulospinose genus *Hantkenina* was paralleled by a shift from a deep- to a shallow-water habitat (Coxall et al. 2000), although modified extensions of the chambers, in the form of narrow non-perforate tubulospines, were retained in younger surface-dwelling forms. Modern digitate species, on the other hand, appear to be more closely related to surface and intermediate-depth dwellers (e.g., *H. pelagica* and *Globigerinella* spp. [Hemleben et al. 1989; M. Kucera personal communication 2007]), suggesting that different selection pressures were responsible for evolution of digitate morphologies in the late Neogene.

The isotopic data and distribution patterns presented here provide an environmental correlate with digitate morphologies—life in deep, DIC-enriched, and possibly regularly oxygen-depleted watermasses associated with increased marine production. This iterative evolution very likely reflects common functional constraints that could be regarded as representing an adaptive process, even though we might not know their exact function or be able to demonstrate the pathway of speciation. By this we mean that digitate chambers, arising through natural variation, are efficient for survival under certain environmental conditions and, therefore, are ''maintained'' or ''selected for'' when these conditions occur, while ineffective characters are eliminated. This is a remarkable finding because few other structural convergences among planktonic foraminifera have been found to correlate with similar ecologies between independently evolved genera and across multiple epochs.

Summary and Conclusions

Digitate planktonic foraminifera morphologies have evolved multiple times over the past 130 million years. Previous studies have hinted that some digitate homeomorphs had similar depth habitats, but our stable isotope results provide the first evidence of a clear correlation between this morphology and a subsurface habitat over multiple epochs.

These findings are consistent with plankton tow data that suggest that all modern digitate species spend part of their life cycle living at mesopelagic or bathypelagic habitats. Geological and modern evidence also links some digitate species with increased marine productivity and low-oxygen environments, but they appear to like strong, quasi-permanent OMZ conditions such as those that developed on the eastern sides of the major ocean basins and in equatorial upwelling systems. The need for these persistent OMZ conditions may explain why these species do not occur in the temperate and high latitudes today but were common during Cretaceous OAEs. However, digitate species are not always associated with regions and episodes of eutrophication and low oxygen concentration, suggesting there are additional physio-chemical and biological controls on their distribution, such as temperature, salinity, nutrients, type of food, and trace elements. We suggest that the function of elongate chambers is primarily a feeding adaptation that allows the foraminifera to search a larger volume of water for food at minimum metabolic cost in a usually food-poor mesopelagic environment. There also appears to be an element of opportunism in the ecology of digitate species, allowing them to proliferate and diversify under certain environmental conditions that are unfavorable to many other planktonic species. As has been suggested for Cretaceous OAE digitates (Coccioni et al. 2006), relative abundance of digitate species may be proportional to the strength of the environmental perturbation related to the OAEs.

Our findings suggest that digitate planktonic foraminifera may be used as a proxy for intervals of expansion of the OMZ, especially during Mesozoic and early Cenozoic greenhouse climates when thermal and density stratification may have been weaker and episodes of widespread eutrophication were more frequent. Further insight into digitate ecologies and environmental preferences can be obtained by studying the ecology of modern digitate taxa, starting with the systematic assessment of *Hastigerinella digitata* distribution in Monterey Bay, and building an expanded database on the isotopic paleoecologies and biogeographic distribution of digitate species over time.

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Appendix

Stable isotope data and sample information. * indicates C^{14} ages converted to calendar years. See Table 1 for age-date sources.

Sample	Period	Biozone/a	Species	$\delta^{13}C$	$\delta^{18}O$	Data source	Size fraction	No.
DSDP-137-12-5, 4–6 cm	Cenomanian	KS17	*''Hedbergella'' simplex*	1.45	−2.99	This study	>112	
DSDP-137-12-5, 4–6 cm	Cenomanian	KS17	*Rotalipora brotzeni*	1.77	−2.60	This study	250–300	
DSDP-137-12-5, 4–6 cm	Cenomanian	KS17	*Rotalipora* cf. *brotzeni*	1.61	−3.08	This study	250–300	
DSDP-137-12-5, 4–6 cm	Cenomanian	KS17	*Praeglobotruncana stephani*	2.05	−2.97	This study	250–300	
DSDP-137-12-5, 4–6 cm	Cenomanian	KS17	*Praeglobotruncana delrioensis*	1.95	−3.20	This study	250–300	
DSDP-137-12-5, 4–6 cm	Cenomanian	KS17	*Hedbergella delrioensis*	2.04	−3.47	This study	250–300	
DSDP-137-12-5, 4–6 cm	Cenomanian	KS17	*Hedbergella planispira*	1.93	−4.00	This study	250–300	
DSDP-137-12-5, 4–6 cm	Cenomanian	KS17	*Globigerinelloides ultramicrus*	1.63	−3.57	This study	250–300	
DSDP-137-12-5, 4–6 cm	Cenomanian	KS17	*Gyroidinoides* sp.	0.40	−1.84	This study	250–300	
DSDP-137-12-5, 4–6 cm	Cenomanian	KS18	*Gavellinella* sp.	0.50	−1.85	This study	250–300	
DSDP-144A-6-1, 141.5–142.5 cm	Cretaceous, Turonian	NP-UC9a	*Heterohelix globulosa*	0.21	−3.89	Wilson et al. 2002	65–125	25
DSDP-144A-6-1, 141.5–142.5 cm	Cretaceous, Turonian	NP-UC9a	*Heterohelix globulosa*	0.38	−4.14	Wilson et al. 2002	65–125	18
DSDP-144A-6-1, 141.5–142.5 cm	Cretaceous, Turonian	NP-UC9a	*Hedbergella delrioensis*	0.86	−4.36	Wilson et al. 2002	65–125	25
DSDP-144A-6-1, 141.5–142.5 cm	Cretaceous, Turonian	NP-UC9a	*Hedbergella delrioensis*	0.63	−4.03	Wilson et al. 2002	65–125	16
DSDP-144A-6-1, 141.5–142.5 cm	Cretaceous, Turonian	NP-UC9a	*Hedbergella amabilis*	0.70	−4.22	Wilson et al. 2002	65–125	16
DSDP-144A-6-1, 141.5–142.5 cm	Cretaceous, Turonian	NP-UC9a	*Heterohelix moremani*	−0.15	−3.95	Wilson et al. 2002	65–125	14
DSDP-144A-6-1, 141.5–142.5 cm	Cretaceous, Turonian	NP-UC9a	*Clavihedbergella watersi*	0.26	−3.29	Wilson et al. 2002	65–125	10
DSDP-144A-6-1, 75–76 cm	Cretaceous, Turonian	NP-UC9a	benthic-1	−0.88	−0.84	Wilson et al. 2002	65–125	10
DSDP-144A-6-1, 75–76 cm	Cretaceous, Turonian	NP-UC9a	benthic-2	−1.44	0.60	Wilson et al. 2002	65–125	9
Kane-9, Core 42, 42 cm	Topmost lower Eocene	P8-P9	*Morozovella lensiformis*	2.91	−0.37	This study	355–400	6
Kane-9, Core 42, 42 cm	Topmost lower Eocene	P8-P9	*Acarinina aspensis*	2.90	−0.82	This study	355–400	5
Kane-9, Core 42, 42 cm	Topmost lower Eocene	P8-P9	*Acarinina bullbrooki*	2.89	−0.64	This study	355–400	5
Kane-9, Core 42, 42 cm	Topmost lower Eocene	P8-P9	*Subbotina* cf. *frontosa*	1.06	0.32	This study	250–300	6
Kane-9, Core 42, 42 cm	Topmost lower Eocene	P8-P9	*Parasubbotina griffinae*	0.49	0.68	This study	250–300	6
Kane-9, Core 42, 42 cm	Topmost lower Eocene	P8-P9	*Parasubbotina griffinae*	0.50	0.64	This study	250–300	6
Kane-9, Core 42, 42 cm	Topmost lower Eocene	P8-P9	*Clavigerinella akersi*	0.45	−0.05	This study	Broken chambers	3
Kane-9, Core 42, 42 cm	Topmost lower Eocene	P8-P9	*Globigerinatheka senni*	1.61	−1.21	This study	212–250	12
Kane-9, Core 42, 42 cm	Topmost lower Eocene	P8-P9	*Globanomalina chapmani*	1.13	−0.24	This study	125–250	16
Kane-9, Core 42, 42 cm	Topmost lower Eocene	P8-P9	*Cibicidoides* sp.	0.61	0.55	This study	250–400	4
Kane-9, Core 42, 42 cm	Topmost lower Eocene	P8-P9	*Morozovella caucasica*	3.20	−0.97	This study	355–400	6
Kane-9, Core 42, 42 cm	Topmost lower Eocene	P8-P9	*Acarinina bullbrooki*	2.45	−1.35	This study	300–355	6
Kane-9, Core 42, 42 cm	Topmost lower Eocene	P8-P9	*Globigerinatheka senni*	1.35	−1.53	This study	212–300	9
Kane-9, Core 42, 42 cm	Topmost lower Eocene	P8-P9	*Subbotina* sp.	1.79	−1.03	This study	212–300	4
Kane-9, Core 42, 42 cm	Topmost lower Eocene	P8-P9	*Clavigerinella colombiana*	0.56	−0.13	This study	Broken chambers	6
Kane-9, Core 42, 42 cm	Topmost lower Eocene	P8-P9	*Clavigerinella akersi*	0.48	−0.20	This study	Broken chambers	6
Kane-9, Core 42, 42 cm	Topmost lower Eocene	P8-P9	*Cibicidoides* sp.	0.77	0.41	This study	250–400	3
ODP-865C-8H-3, 70–72 cm	Topmost lower Eocene	P9-P10	*Clavigerinella eocanica*	1.11	0.20	Coxall et al. 2003	>250	3
ODP-865C-8H-3, 70–72 cm	Topmost lower Eocene	P9-P10	*Acarinina pseudotopilenis*	3.19	−1.20	Coxall et al. 2003	250–300	5
ODP-865C-8H-3, 70–72 cm	Topmost lower Eocene	P9-P10	*Subbotina frontosa*	1.77	−0.27	Coxall et al. 2003	250–300	5
ODP-865C-8H-3, 70–72 cm	Lower/middle Eocene	P9-P10	*Cibicidoides* sp.	0.49	0.40	Coxall et al. 2003	250–300	2
ODP-865C-8H-3,110–112 cm	Lower/middle Eocene	P9-P10	*Clavigerinella eocanica*	1.56	0.35	Coxall et al. 2003	>250	2
ODP-865C-8H-3,110–112 cm	Lower/middle Eocene	P9-P10	*Morozovella aragonensis*	3.56	−1.20	Coxall et al. 2003	250–300	4
ODP-865C-8H-3,110–112 cm	Lower/middle Eocene	P9-P10	*Acarinina pseudotopilenis*	3.02	−0.80	Coxall et al. 2003	250–300	6
ODP-865C-8H-3,110–112 cm	Lower/middle Eocene	P9-P10	*Subbotina frontosa*	1.71	−0.30	Coxall et al. 2003	250–300	6
ODP-865C-8H-3,110–112 cm	Lower/middle Eocene	P9-P10	*Cibicidoides* sp.	0.83	−0.10	Coxall et al. 2003	250–300	3
ODP-865C-8H-3,110–112 cm	Lower/middle Eocene	P9-P10	*Guembelitrioides nuttali*	2.39	−0.40	Coxall et al. 2003	250–300	5

Appendix. Continued.

Sample	Period	Biozone/a	Species	$\delta^{13}C$	$\delta^{18}O$	Data source	Size fraction	No.
ODP 865B-8H-4, 137–139 cm	Lower/middle Eocene	P9-P10	*Parasubbotina eoclava*	1.19	−0.77	Coxall et al. 2003	250–300	3
ODP 865B-8H-4, 137–139 cm	Lower/middle Eocene	P9-P10	*Morozovella spinulosa*	2.90	−1.93	Coxall et al. 2003	250–300	7
ODP 865B-8H-4, 137–139 cm	Lower/middle Eocene	P9-P10	*Acarinina pseudotopilensis*	3.06	−1.69	Coxall et al. 2003	250–300	5
ODP 865B-8H-4, 137–139 cm	Lower/middle Eocene	P9-P10	*Subbotina frontosa*	1.34	−1.08	Coxall et al. 2003	250–300	5
ODP-872C-9H-2, 95–97 cm	Middle Miocene	N10	*Clavatorella bermudezi*	1.60	0.55	This study	>250	2
ODP-872C-9H-2, 95–97 cm	Middle Miocene	N10	*Globoquadrina venezuelana*	1.97	−0.71	This study	>250	7
ODP-872C-9H-2, 95–97 cm	Middle Miocene	N10	*Globigerinoides ruber*	2.41	−2.85	This study	>250	12
ODP-872C-9H-2, 95–97 cm	Middle Miocene	N10	*Globorotalia peripheroronda*	1.88	−2.64	This study	>250	22
ODP-872C-9H-2, 95–97 cm	Middle Miocene	N10	*Clavatorella bermudezi*	1.86	0.33	This study	>250	3
ODP-872C-9H-2, 95–97 cm	Middle Miocene	N10	*Globoquadrina venezuelana*	2.15	−0.35	This study	>250	11
ODP-872C-9H-2, 95–97 cm	Middle Miocene	N10	*Globigerinoides ruber*	2.85	−2.07	This study	>250	17
ODP-872C-9H-2, 95–97 cm	Middle Miocene	N10	*Globorotalia peripheroronda*	1.62	−2.73	This study	>250	14
ODP-872C-9H-2, 95–97 cm	Middle Miocene	N10	*Clavatorella bermudezi*	1.59	0.08	This study	>250	3
ODP-872C-9H-2, 95–97 cm	Middle Miocene	N10	*Globoquadrina venezuelana*	1.71	−0.79	This study	>250	16
ODP-872C-9H-2, 95–97 cm	Middle Miocene	N10	*Globigerinoides ruber*	2.87	−2.20	This study	>250	14
ODP-872C-9H-2, 95–97 cm	Middle Miocene	N10	*Globorotalia peripheroronda*	1.84	−2.08	This study	>250	7
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Cibicidoides wuellerstorfi*	0.29	2.35	Berger et al. 1978	400–600	3
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Cibicidoides wuellerstorfi*	0.28	2.98	Berger et al. 1978	400–600	3
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Globigeriniodes sacculifer*	1.44	−1.62	Berger et al. 1978	400–600	5
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Globigeriniodes sacculifer*	1.66	−1.32	Berger et al. 1978	400–600	5
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Globigeriniodes sacculifer*	1.94	−1.47	Berger et al. 1978	400–600	5
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Globorotalia menardii*	0.69	−1.02	Berger et al. 1978	400–600	3
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Globorotalia menardii*	1.51	−0.05	Berger et al. 1978	400–600	3
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Globorotalia menardii*	1.73	−0.46	Berger et al. 1978	400–600	4
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Globorotalia tumida*	1.94	0.04	Berger et al. 1978	400–600	3
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Globorotalia tumida*	2.06	−0.18	Berger et al. 1978	400–600	3
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Globorotalia tumida*	2.02	0.02	Berger et al. 1978	400–600	4
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Neogloboquadrina pachyderma*	0.78	−0.56	Berger et al. 1978	400–600	4
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Neogloboquadrina pachyderma*	1.34	−0.41	Berger et al. 1978	400–600	4
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Neogloboquadrina pachyderma*	1.26	−0.47	Berger et al. 1978	400–600	4
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Pulleniatina obliquiloculata*	1.11	−1.00	Berger et al. 1978	400–600	5
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Pulleniatina obliquiloculata*	1.02	−0.98	Berger et al. 1978	400–600	5
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Pulleniatina obliquiloculata*	1.14	−0.77	Berger et al. 1978	400–600	4
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Globigerinella adamsi*	−0.12	−0.41	This study	>400	1
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Globigerinella adamsi*	−0.18	−1.05	This study	>400	2
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Globigerinella* cf. *adamsi*	−0.39	−0.19	This study	>400	2
Box-core EDRC-92-5, 22–23 cm	Upper Pleistocene	14.2 ka*	*Globigerinella* cf. *adamsi*	−0.36	−1.15	This study	>400	2
Core CD154-07-7PK core top	Holocene	—	*Beella digitata*	0.28	0.80	This study	>250	5
Core CD154-07-7PK core top	Holocene	—	*Beella digitata*	0.15	0.87	This study	>250	5
Core CD154-07-7PK core top	Holocene	—	*Globorotalia tumida*	1.33	−0.70	This study	>250	1
Core CD154-07-7PK core top	Holocene	—	*Globorotalia truncatulinoides*	1.27	0.54	This study	>250	3
Core CD154-07-7PK core top	Holocene	—	*Globorotalia truncatulinoides*	0.90	0.24	This study	>250	1
Core CD154-07-7PK core top	Holocene	—	*Globigeriniodes sacculifer*	1.63	−1.78	This study	>250	2
Core CD154-07-7PK core top	Holocene	—	*Globigerinoides ruber*	0.96	−1.83	This study	>250	2
Core CD154-07-7PK core top	Holocene	—	*Neogloboquadrina deutertrei*	1.51	−0.92	This study	>250	4
Core CD154-07-7PK core top	Holocene	—	*Cibicidoides wuellerstorfi*	0.88	2.14	This study	>250	3
Core CD154-07-7PK core top	Holocene	—	*Cibicidoides wuellerstorfi*	0.84	2.20	This study	>250	8